JOURNAL
OF THE
BOMBAY NATURAL HISTORY
SOCIETY

April 1991 Vol. 88 No. 1

BREEDING BIOLOGY OF THE YELLOWBROWED LEAF WARBLER *PHYLLOSCOPUS INORNATUS* IN KASHMIR[1]

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(With a plate and eight text-figures)

The yellowbrowed leaf warbler *Phylloscopus inornatus* is a small (6 g) warbler which breeds from the Urals to central China as far south as the Himalayas, and winters in India and south-east Asia (Dementiev and Gladkov 1968, Williamson 1974, Ali and Ripley 1983). One subspecies (*P. i. humei*) breeds abundantly in Kashmir (Hume and Oates 1889, Bates and Lowther 1952, Price and Jamdar 1990). The nest and eggs of the species have been described by several authors (Hume and Oates 1889, Bates and Lowther 1952, Dementiev and Gladkov 1968, Ali and Ripley 1983), but despite its abundance other aspects of its breeding biology are poorly known. In this paper we describe the breeding behaviour of the species based on a study over three summers (1985-1987) at one locality in Kashmir. We present information on general breeding behaviour, clutch and brood sizes, and factors affecting nest success.

Phylloscopus inornatus breeds 1-3 weeks earlier in the season than other species of *Phylloscopus* at this locality (Price and Jamdar in press) and often encounters harsh weather conditions during egg-laying and early incubation. We will use information on nesting and feeding behaviour to ask how this species is able to breed so early, and also consider the selective factors which may have favoured early breeding.

STUDY AREA AND METHODS

Our study was conducted at the Overa Wildlife Sanctuary, a small (33 sq. km) reserve located near Pahalgam, Kashmir. A description of the habitats, location, and summer climate at the Sanctuary is given by Price and Jamdar (1990). We spent from May-July in each year 1985, 1986 and 1987, at the Sanctuary. In 1985 we first established a study area near the entrance to the Sanctuary in coniferous forest at an altitude of *c.* 2,500 m. In June that year we discovered *P. inornatus* breeding abundantly in the birch woods which grow above the coniferous forest and form the treeline (*c.* 3,300-3,500 m altitude). Subsequently we camped at about 3,300 m except during periods of inclement weather in May 1986 and May 1987. In 1985 we established a single study area (UP1). In 1986 and 1987 we also studied a second area (UP2), about 2 km distant from the first, with one of us based at each of the localities (Price and Jamdar 1990).

Breeding biology: Methods used varied from year to year, and differed between the two study areas. In 1985 we only discovered the breeding grounds when most birds were incubating clutches of eggs. We concentrated on finding nests and documenting nesting success. This was the main focus of the study at UP2 in 1986 and 1987, although many nests were monitored from the beginning of nest building. In

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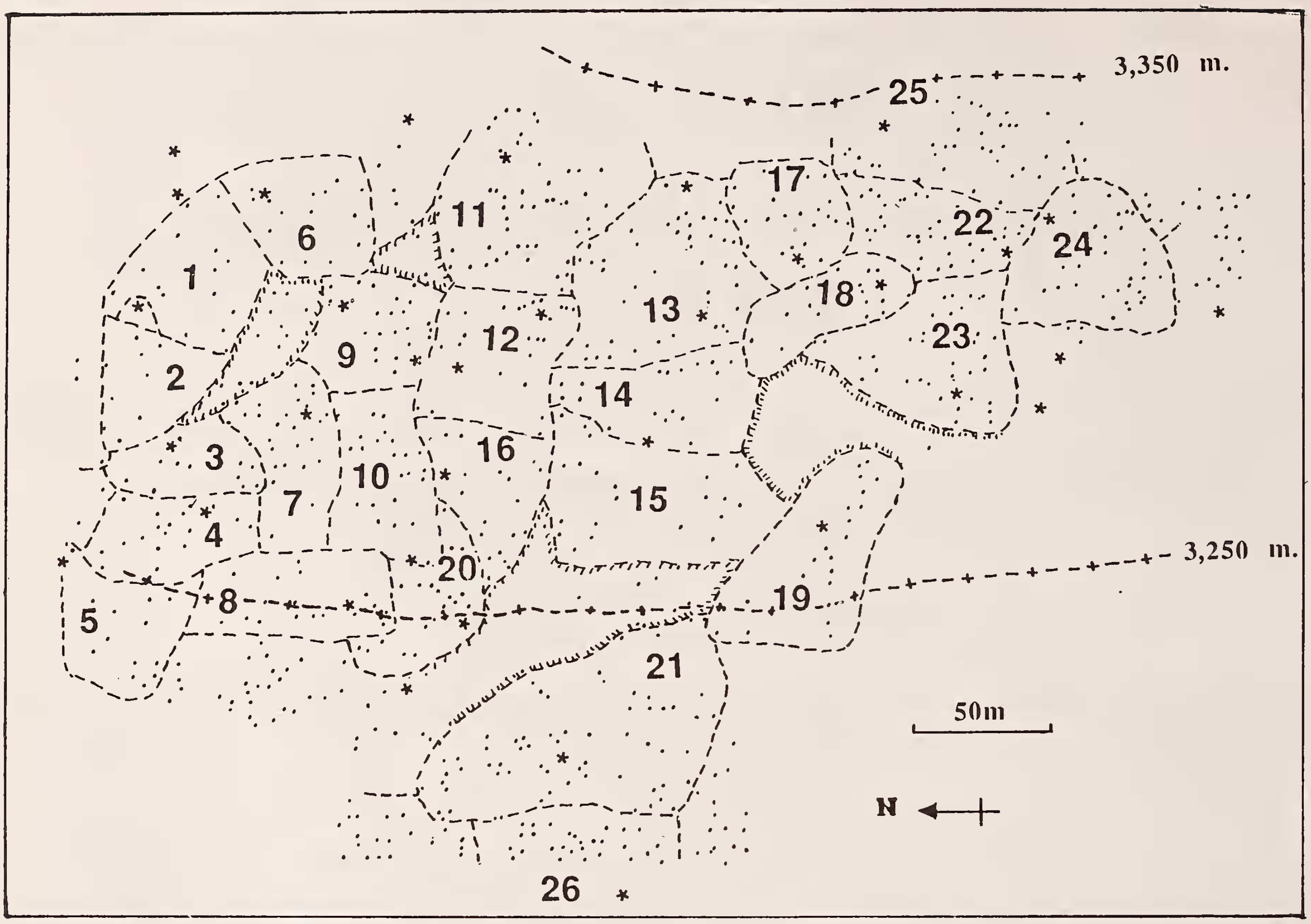


Fig. 1. Territories of *P. inornatus* over an area of birch woodland at UP1. Inwardly shaded areas mark areas that were apparently not defended. The woodland is continuous at the edges. Territory 17 was taken over by Male 13 expanding his territory on 18 June. Distances are measured along the ground: note from the contours (– +–) that the terrain is very steep. Each dot marks a mapped tree (>5m height). Nests are marked with an asterisk (*).

1986 at UP1, in addition to finding nests we made observations on courtship and feeding behaviour.

In 1987 at UP1 we trapped most of the males and females over a 10 ha. area prior to breeding. The birds were given a single metal ring and a single colour ring which enabled them to be subsequently individually identified. Then, during the pre-laying and incubation periods we mapped the territories of 24 males by intensively following them or watching individual trees and waiting for a male to sing in them (Fig. 1.) A male was considered to 'own' a tree if it was observed singing in it, and we never recorded two males singing in the same tree, except when one male was in the process of usurping the territory of another.

With the territories mapped we were able to search for a nest for every territory. At UP2 and in other years at UP1 we were unsure of nest density, and made no special effort to locate all the nests in a given area. All trees in the area covered by the mapped territories at UP1 were themselves mapped using a tape and compass, and individually marked with numbered metal tags.

We discovered a total of 349 nests over the 3 years of the study, mostly by watching the females carrying nest material during building and going on to the nest during incubation, and both parents when feeding the young. Nests were marked with a piece of flagging tape (red in the first two years; subsequently, when we realised crows were recognising the tapes and preying on nests, a very small green piece some distance away from the nests). Nests were checked infrequently to determine clutch and brood sizes and hatching and fledging dates. Chicks were ringed with a single numbered metal ring and weighed and measured approximately 11 days after hatching.

In connection with a separate study (Price in prep.) hatchling chicks from many broods in 1986 and 1987 were exchanged between nests. Between one and three chicks were removed from one nest on the day of hatching, and placed in a second nest, with a corresponding number from the second nest placed in the first. In cases where this manipulation could have affected the results we report in this paper, we analysed the data separately for all broods, and for the subsection of broods which went unmanipulated.

Feeding behaviour: *P. inornatus* is entirely insectivorous. Feeding behaviour was recorded whenever possible. Since it is difficult to keep birds in sight for long, particularly in June and July when the birch trees are in leaf, quantitative observations were largely confined to recording a single feeding event for one individual, and then searching for another individual. We distinguished between four different feeding methods: 1. *Flycatch:* when a bird captures a flying insect, often one it has disturbed. 2. *Flypick:* when a bird captures an insect from a leaf or branch by flying for it. 3. *Hoverpick:* when the bird hovers in front of a leaf before picking up the insect. 4. *Standpick*: when a bird picks up an insect from the substrate without flying. We also recorded the size and type of prey whenever it was visible.

Arthropod abundance: Seasonal changes in arthropod abundance were quantified in two ways. First, we placed white bowls (*c*. 20 cm in diameter) half filled with water and detergent for periods of 1-6 days at selected locations in the study area. All arthropods which fell into the bowls were counted and sorted by size class and order. Second, we regularly beat birch branches with a stick, and collected all arthropods which fell into a tray held below the branch. A single sample usually consisted of the arthropods collected from 20 beats on a total of 6-15 birch trees in a small area.

RESULTS

Distribution of *P. inornatus:* The breeding of *P. inornatus* appears to be intimately associated with the presence of broad leaf trees, particularly the silver birch *Betula utilis*. In pure birch stands above 3,300 m it occurs abundantly, in densities as high as 4 pairs per ha. in some areas (Fig. 1). It is by far the commonest breeding bird in the birch woods (Price and Jamdar 1990). It does not breed in, or along the edge of, the coniferous woods found between about 2,400 m and 3,300 m (contra statements of Bates and Lowther 1952, Williamson 1974).

A few pairs may breed in the stands of deciduous trees (notably walnut *Juglans regia*, cherry *Prunus cornuta*, and chestnut *Aesculus indica*) found along the rivers and around the villages at lower altitudes (Hume and Oates 1889). Our evidence in support of this is not conclusive: it is based on the presence of singing males throughout the day early in the breeding season (although they were not noted on our few visits to this altitude in June), and observations of a parent feeding a recently fledged juvenile at that altitude in July 1985.

Songs and call notes: As a prelude to describing the breeding behaviour we first classify the various vocalisations of this species. There are two distinctive songs (Martens 1980 gives sonagrams). The first song is a double noted *dioo dioo*, and the second a thin declining buzz, lasting about one second. The songs are used in different contexts. The first song is used commonly in territorial defence and advertisement: it is, for example, essentially the only song heard in the dawn chorus. The buzz is heard 1) at the end of some sequences of the first song, particularly when the female is nearby, 2) in rain and at dusk early in the season, and 3) after nests have been predated, or the female has disappeared. Both songs are also used in winter quarters; their significance in the non-breeding season merits a detailed investigation.

In addition to the songs there are a number of call notes in the breeding season. The commonest is a single alarm note, *dioo*, similar to one syllable of the first song, uttered by both sexes. A run-together version of rapid repeats of the alarm note is heard whenever avian predators or cuckoos fly over, given most often by the males during the early phases of the nesting period. Birds in the neighbourhood take cover, and nearby males take up the alarm call. The female has a *wheet wheet* call that she often utters when leaving a nest under construction, or when faced by a male who is not her mate. Finally both sexes 'chupper', a series of soft notes given between the pair when they are in close proximity, and the female is about to go to the nest. It appears to be a form of appeasement and it is uttered continuously during sex chases (chases of the female by the male over the territory). Chuppering also rarely occurs during male-male interactions.

Territory establishment: Males were found singing on territory from the time we arrived at the study area in early May 1986 and 1987. Initial territory establishment thus probably occurred before our arrival. In both years, several feet of snow were on the ground and the birch trees did not come into leaf until June. On most days males were present only in the early morning and deserted the area, apparently for lower altitudes, within a few hours after dawn. Individuals were only rarely seen in the afternoon. In May of both years there were days with rain, hail, and snow storms and temperatures near freezing (Price and Jamdar 1990). In these periods of inclement weather no *P. inornatus* individuals were present throughout the day.

We have not knowingly observed either initial territory establishment or initial pair formation. Prior to earnest nest building, and in the first hour or so after dawn, females are commonly seen visiting bare patches of ground, investigating suitable hollows, and occasionally picking up items of potential nest material. Males join their females and commonly may engage in long sex chases. The males also spend time off territory. Both females and males were seen to chase off intruding conspecifics. Wing flicking is common, and wing drooping in concert with the song also occurs, but most of the displays appear quite simple. The slow flutter flights recorded commonly in *Phylloscopus trochilus* in Europe (May 1949) were observed only once, and there is no elaborate wing waving as occurs in *P. occipitalis*. When agitated, for example by playback of tape recorded song, the male droops and shivers his wings and cocks his tail.

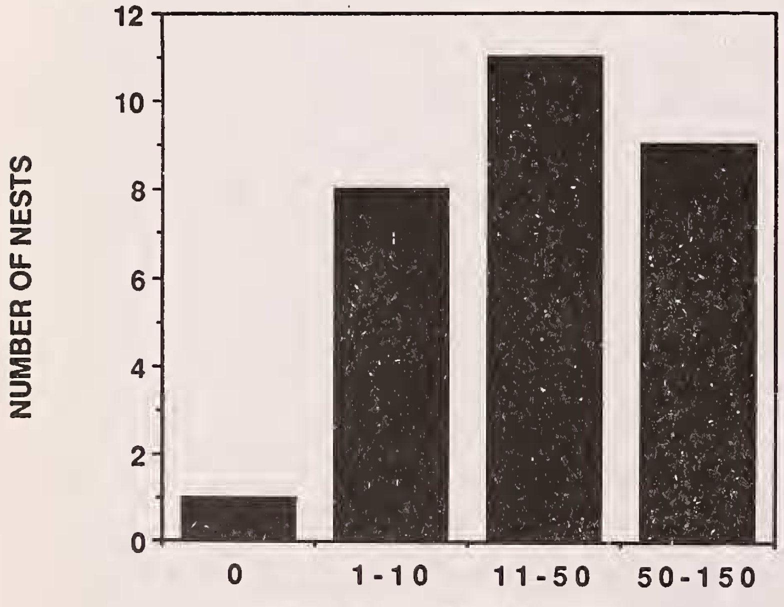


Fig. 2. Distribution of the number of mammal hairs in nests of *P. inornatus* (N = 25 carefully checked nests).

TABLE 1

LOCATIONS OF THE NESTS OF *P. inornatus*

Proportion on:	
Ledge*	38%
Slope	62%
Proportion in shade of[1]:	
Birch	49%
Fir	11%
Juniper	6%
Rhododendron	9%
No shade tree	25%
Dominant nearby vegetation[2]:	
Grass	60%
Bush	23%
Leaf Litter	17%

Based on N = 47 nests at UP1 in 1987. *A ledge is defined as the presence of a rockface below the nest within 0.5 m. [1]A tree is defined as shading the nest if its canopy lies vertically above the nest. [2]Vegetation within 50-100 cm of the nest.

We witnessed few fights. The most serious occurred at a time when most pairs were in the incubation phase. An individual expanded his territory, and expelled a neighbour. He was first observed in several close chases with the neighbour, before engaging in a full fight. We never observed the male feeding his mate.

Copulation is secretive: we only observed it on two occasions on 9 June, 1986, in a birch tree. Copulation was preceded by a long sex chase, with both birds of the pair wing flicking and holding their tails slightly cocked when perched. Adjoining pairs were excited at this time, and there was a great deal of interaction among neighbouring individuals, although the sexes could not be readily distinguished.

Territory characteristics: Fig. 1 shows a territory map for an area at UP1. Despite intensive watches a few areas were never seen to be visited by singing males. One or two other areas (notably a large part of the area covered by male 21) were only seen to be visited by the male once, and may not have been actively defended. The average territory area, as measured directly from this map is 2,030 ± 806 sq. m which is smaller than the size recorded for European *Phylloscopus* (Edington and Edington 1972, Lawn 1982, Tiainen 1983, Temrin *et al.* 1984), and the average territory contains 21 ± 11.6 trees. Approximately 20% of the trees in the area are conifers (Price and Jamdar 1990). Although territories may contain none or many conifers, they always

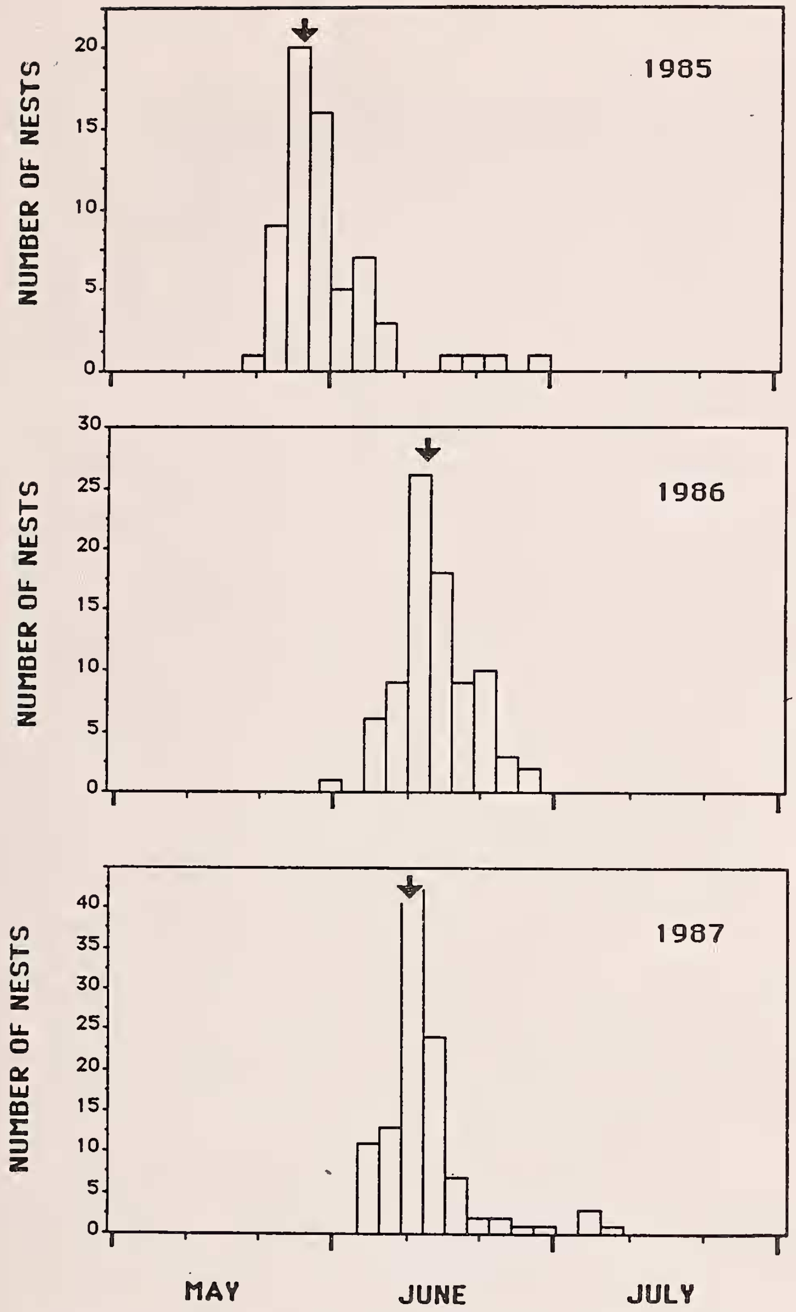


Fig. 3. Date of first eggs in nests in each of the three years of study. When clutch initiations were not observed the initiation date was back calculated from hatching or fledging date assumming 1) eggs are laid consecutively 2) a 16 day incubation period from the laying of the last egg and 3) 12 days to fledging. The incubation period used is shorter than the median incubation period for known nests (19 days), but distributions of accurately known clutch initiation dates in 1986 and 1987 were similar to those presented here. Few initiation dates were known in 1985.

contain at least one birch tree. Pure conifer stands are not occupied. We have never found an exception to this either in other years or at the other site.

Breeding system: The breeding system is largely monogamy. All 24 males in the mapped area of 1987 were known to have a mate, and at least two were known to be bigamous. Since it is difficult to be sure that all nests were found it is possible that there were more bigamous pairings. Laying dates of the two females in each of the two bigamous pairings were 1 day and 9 days apart. Unfortunately, three of the four nests in the bigamous pairings were predated prior to hatching, so it was not possible to ascertain the males' roles in raising the young. In two European species of *Phylloscopus* warbler *P. trochilus* and *P. sibilatrix*, males are known to set up secondary territories once their female is incubating, and may attract a second mate (Lawn 1982, Temrin 1984, Temrin *et al.* 1984). We have no evidence for such poly-territoriality in *P. inornatus* and on the basis of extensive observations think it unlikely. In our study both bigamous males attracted two females to one territory, as is known to occur in *P. trochilus* (Lawn 1982, Tiainen 1983) and in a third *Phylloscopus* species, *P. collybita* (Schonfeld 1978).

Nest building and nest characteristics: The nest is domed. As in other species of *Phylloscopus* only the female builds, although we suspected the male of picking up a stick on one occasion; nest building by both sexes has been observed rarely in other *Phylloscopus* (May 1949; Kovshar and Gavrilov 1974, Merton 1986, Radford 1986). On the first moderately warm day nest building begins in earnest. This occurred on 26 May 1986 and 30 May 1987 but must have occurred at least two weeks earlier in 1985. Nest building halts in bad weather. Of the 349 nests located all have been built on the ground or on a cliff face. In Table 1 we present an analysis of the nest locations for the birds in and around the territories of Fig. 1. Nests are often found concealed among the broad leaf perennial plant *Bergenia straychi*, particularly at UP2 where it is common. Three of the nests we found in 1986 were reused in 1987.

Characteristics of some nests were measured at the end of the 1987 breeding season. Average weight was 17.1 ± 4.0 g, range 12-25.5 g (N=38), weight may be overestimated for some nests because of water absorption. Average external width was 115 ± 13 cm and average external height 101 ± 11 cm (N = 33). The major constituent of the nest is grass. In addition 72% contained some birch bark, and 79% contained some moss (N=33). Pine needles were recorded in some other nests. A remarkable feature of these nests is their lining which, as Hume and Oates (1889), noted consists of thin grass and often mammal hairs (Fig. 2), but never feathers. The hairs in our nests were long and grey. Hume and Oates suggest the hair may come from horse or musk deer *Moschus moschiferus*, but neither of these species were observed in the vicinity of UP1 (al-

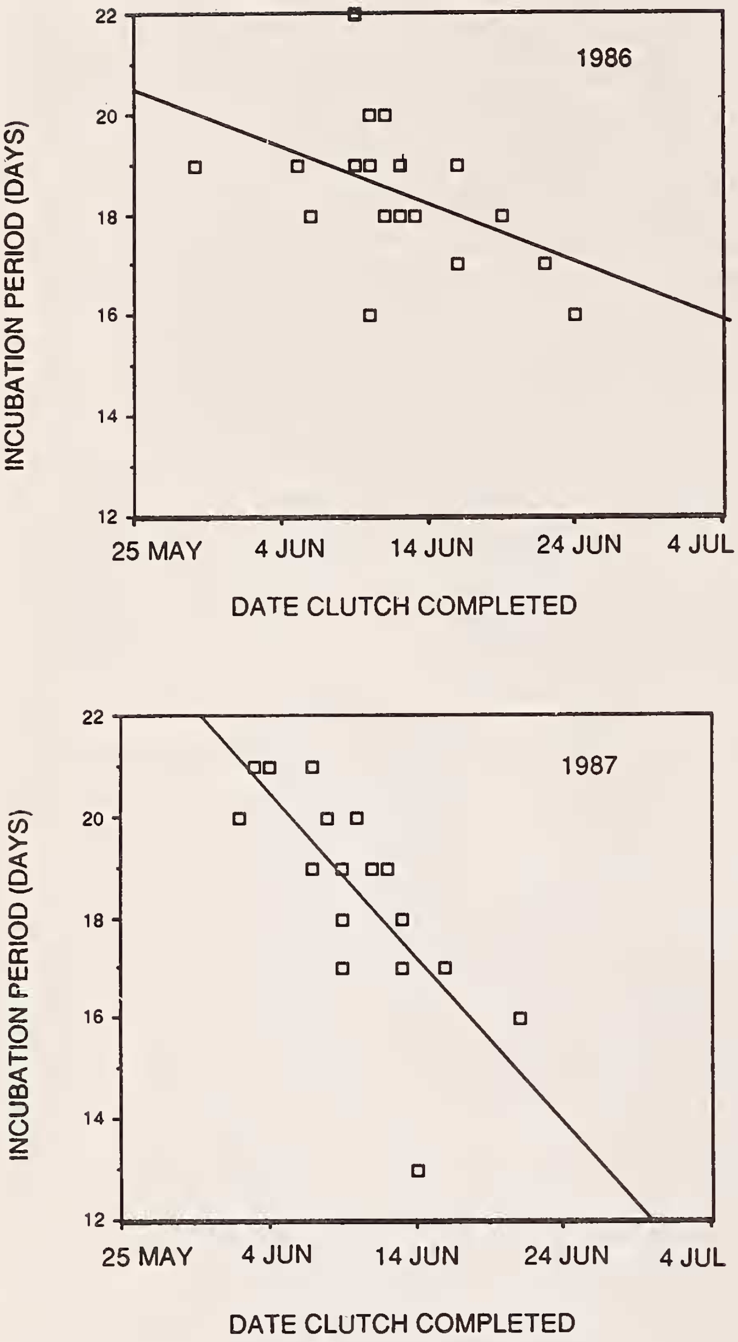


Fig. 4. Association between incubation period (number of days between clutch completion and hatching) with day of laying in the season. Linear regression lines are shown. The slopes are, for 1986: b = – 0.11: F (1,16) = 5, P<0.05,
for 1987: b = – 0.33; F (1, 18) = 24, P<0.001.

though both these mammals and goats and cows were at UP2, where the nests were not examined in detail). One female at UP2 was seen flying a long distance into cow pasture to collect hairs. The Himalayan langur *Presbytis entellus* is common at both study areas, and may provide some of the hairs.

Laying and incubation: We found some nests as they were just beginning to be built, and from this can ascertain the interval between construction and laying. The longest recorded interval between commencement of building and laying was 16 days (30 May 1987, when the nest was well under construction, to 14 June). The interval varies and another female building a nest at the same stage on the same day laid her first egg on 5 June. The shortest recorded interval between depositing the first straw and laying was 5 days (17-22 June). This female had deserted her first nest after interference with her mate from a neighbouring male (see Fig. 1 caption), and built the new nest very rapidly.

The date of laying the first egg varied among females by more than 30 days in each year, although the bulk of the initiations occurred within 20 days of each other (Fig. 3). Later initiations may reflect relaying after early predation or desertion for other reasons. The median initiation date was 27 May 1985, 13 June 1986 and 10 June 1987. Initiation was therefore about two weeks earlier in 1985 than in the other two years. This presumably was in response to the better weather, and less standing snow in that year (Price and Jamdar 1990).

We visited five nests twice during the laying phase. In all of these nests eggs were laid on consecutive days. Incubation appeared to begin with the last egg, and eggs hatched within a day of each other. The earliest breeding females may continue to vacate the study area during the laying period, and only visit the nest and vicinity in the early morning to lay an egg. On 1 June, 1986 we watched a nest containing three eggs for 30 minutes at dusk and saw no sign of the pair. The female was observed arriving the next day after dawn to lay a fourth egg.

Incubation is entirely by the female. The presence of a brood patch was a definitive way to sex a bird in the hand as female, and observations on colour ringed birds confirm that the male never enters the nest. Once incubation begins both the female and male appear to reside on territory. However, in severe rain or hail, at least during early incubation, all birds may vacate the area for periods of at least 36 hours. We discovered this in 1986 when females left their nests for possibly as long as two days following rainfall on 12 June. One clutch was known to have been deserted for at least 12 hours, after it had been incubated for five days. The female returned and the eggs eventually hatched. In 1987, following heavy rain on the 8th through the 9th June, all incubating females left their nests. Nest temperatures were measured at two nests at 1300 hrs on 9 June by placing a wire thermocouple among the eggs, and allowing the temperature to equilibrate for

TABLE 2
THE PERCENTAGE OF NESTS IN EACH YEAR WHICH HAD 1,2,3,4, OR 5 EGGS WHEN THE CLUTCH WAS APPARENTLY COMPLETE

	Year		
Clutch size (eggs)	1985	1986	1987
1	0	3	2
2	0	3	8
3	11	25	16
4	63	66	70
5	26	2	4
Total number of nests studied	46	88	119

two minutes. Temperatures were 9° C in both nests. Ground temperature around the nest was 11°C, and air temperature 12°C. The nests were clearly not being incubated despite the fact that incubation had gone on for 3 days previously in each case. All females subsequently returned to the area, after at least two nights and one day away, and there was high hatching success in nests that were not predated.

Incubation periods vary greatly, from a minimum of 13 days to a maximum of 22 days (combining 1986 and 1987, X = 18.6 days ± 1.75 , N = 37). The length of the incubation period was significantly negatively correlated with clutch initiation date in both 1986 and 1987 (Fig. 4). A nest that was started ten days later on average took one day less to incubate in 1986, and three days less in 1987 (Fig. 4). The negative correlation of incubation period with laying date presumably reflects the increasing ability of females to continuously incubate eggs as the season progresses, and the weather improves.

Clutch sizes: Clutch sizes ranged from 1-5 eggs, but 1 and 2 egg clutches were rare. No single egg clutches hatched, but at least one was known to be incubated for several days. The distribution of clutch sizes varied among years (Table 2). The average clutch size was 4.2 ± 0.6 in 1985, 3.6 ± 0.8 in 1986, and 3.7±0.8 in 1987. Differences among years were significant (considering only the 3, 4 and 5 egg clutches, $\chi^2 = 28.3$, degrees of freedom = 4, $P < 0.001$), with larger clutches being laid in 1985. In 1986 there was a negative association between clutch size and date of laying in the season (Table 3), but in 1985 and 1987 there was no significant trend. Some of the later-laid small clutches may be repeat clutches after early predation events, although we have no direct evidence for this.

Nestling period: At first the nestlings appear to be largely fed by the male, and the female spends most of her time incubating the young. As the young increase in size the female increases her share, until both sexes appear to be providing food equally, although we made no quantitative observations. Females continue to brood the young at night until they are close to fledging (this is based on an observation of a female entering the nest at dusk, and staying in, and the discovery of adult remains in a nest with 10 day old chicks, probably predated by the Himalayan weasel *Mustela sibirica.* We have recorded fledging at 11-14 days of age but the range may be greater.

Chicks hatch at approximately 0.9 g weight (N=13 chicks weighed on day of hatching in 1986). At time of ringing (i.e. at age *c.* 11 days) the average weight was 7.0 ± 0.7 g (N = 169) in 1985, 7.1 ± 0.7 g (N=171) in 1986, and 7.3 ± 0.6 g (N = 135) in 1987. Unlike the European *Phylloscopus* which appear to grow only to adult size (Tiainen 1978), chicks at ringing are *c.* 15% larger than adult weight. There was significant variation in weight among the three years, ANOVA, F(2,472)=9.9, P< 0.001, with the

TABLE 3
AVERAGE LAYING DATE FOR CLUTCHES OF DIFFERENT SIZES IN EACH YEAR

	Laying date		
	1985 X ± S.D. (N)	1986 X ± S.D. (N)	1987 X ± S.D. (N)
Clutch Size			
3 eggs	29 May ± 5 (5)	16 June ± 5 (15)	12 June ± 5 (17)
4 eggs	31 May ± 8 (26)	13 June ± 5 (53)	11 June ± 5 (65)
5 eggs	1 June ± 10 (12)	9 June ± 1 (2)	9 June ± 4 (4)
F value	0.3	3.7 *	0.5

Average date, standard deviation (in days) and sample size are given. When unknown, laying date was back calculated as in Fig. 3. The F values are for one way analyses of variance among clutch sizes. *P < 0.05.

Table 4
AVERAGE NUMBER OF EGGS IN A CLUTCH, NUMBER OF HATCHLINGS, AND NUMBER OF FLEDGLINGS FOR EACH YEAR

	1985 X ± S.D. (N)	1986 X ± S.D. (N)	1987 X ± S.D. (N)
Clutch size	4.2 ± 0.6 (46)	3.6 ± 0.8 (88)	3.7 ± 0.8 (199)
Hatch size	3.9 ± 0.9 (39)	3.5 ± 0.7 (71)	3.2 ± 0.8 (87)
Fledge size (all broods)	3.9 ± 0.9 (50)	3.2 ± 0.9 (54)	3.0 ± 0.9 (44)
Fledge size (unmanipulated broods)	–	3.4 ± 0.8 (25)	2.8 ± 1.03 (12)

Mean, standard deviation and sample size are given. Localities are combined. Unmanipulated broods refer to those broods which did not not receive chicks from another nest, or donate chicks to a nest at the time of hatching (see methods). In 1985 all broods were unmanipulated.

lightest chicks in 1985, and the heaviest in 1987. Possibly this reflects the fact that brood sizes were smallest in 1987, and largest in 1985 (Table 4), and hence individual chicks could receive more food in 1987.

In 1985 and 1986, the weight of the chicks at ringing was lower later in the season than earlier, but there was no such trend in 1987 (Fig. 5). We noted several very late broods in which chicks had slow growth rates, and may have fledged significantly later. In the last nest to hatch in 1986 the chicks were abandoned by their parents at approximately 7 days of age, and subsequently starved.

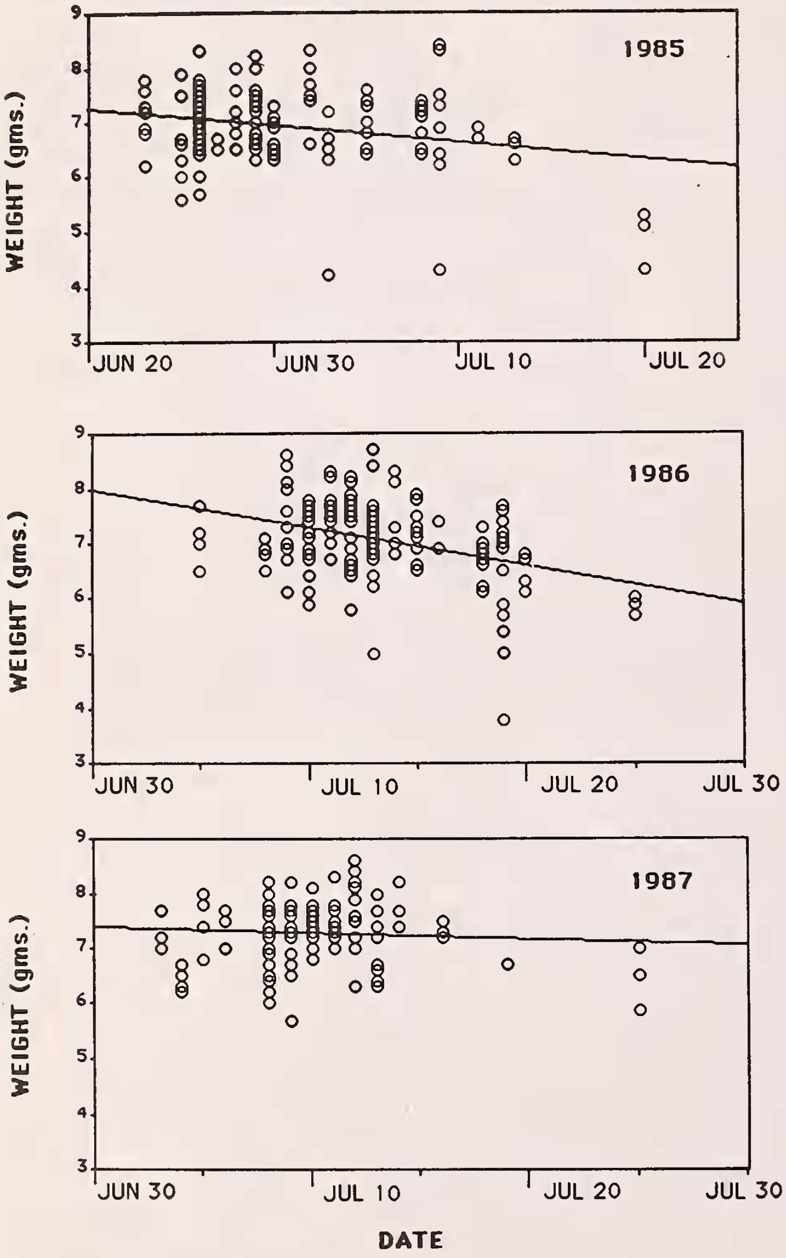


Fig. 5. Weights of chicks at fledging as a function of fledging date.

Hatching and fledging success: Hatchling and fledgling sizes for each year are shown in Table 4. On average there are fewer hatchlings per nest than eggs and fewer fledglings per nest than hatchlings. In 78 nests found prior to laying from which at least one chick hatched, 41% had fewer chicks hatching than eggs laid (some of these nests may have in fact lost a hatchling within a day or two of hatching). This is higher than the 10%-20% typically recorded for passerines (Lundberg 1985). In 155 nests checked at hatching, 52% had fewer chicks fledging than hatched. This figure may be inflated by the experimental manipulations we conducted (swapping hatchlings among nests). In 1985, when we conducted no manipulations, only 18% of the nests (N = 22) had fewer chicks at fledging than hatching. But in 1986 and 1987 brood reduction among unmanipulated broods was 48% (N = 43), similar to the value for all broods, so we conclude that experimental manipulation was not a major cause of brood reduction.

In addition to the loss of individual eggs and nestlings through hatching failure, starvation, etc., lower average fledge sizes than average clutch sizes per nest could be due to heavier predation rates on nests with larger broods, but we show below that there is no association of clutch or brood size with probability of predation (Table 6).

Fledging: Once chicks leave the nest some are fed by the male and some by the female, as commonly occurs in Passerines (McLaughlin and

TABLE 5
NESTING SUCCESS BY PERIOD AND LOCALITY

			Fate of nests			
	Successful fledging	Predated	Deserted	Not successful for other reasons	Unknown	Total
1985, UP1						
Nest found when:						
Building	1	0	0	0	0	1
Laying	1	0	0	0	0	1
Incubation	24	5	1	1	3	34
Young chicks	13	3	0	2	0	18
Old chicks	13	1	0	0	0	14
Total	52	9	1	3	3	68
1986, UP1						
Nest found when:						
Building*	4	14	10 (8)	3	0	31
Laying	1	0	0	1	0	2
Incubation	5	4	1	0	0	10
Young chicks	3	3	0	0	0	6
Old chicks	2	0	0	0	0	2
Total	15	21	11	4	0	51
1986, UP2						
Nest found when:						
Building*	19	2	14(11)	2	4	41
Laying	1	0	0	0	0	1
Incubation	16	7	2	2	0	27
Young chicks	3	2	0	0	0	5
Old chicks	2	1	0	0	0	3
Total	41	12	16	4	4	77
1987, UP1						
Nest found when:						
Building*	13	8	6(4)	1	1	29
Laying	3	1	1	0	0	5
Incubration	8	7	1	1	0	17
Young chicks	0	3	0	0	0	3
Old chicks	1	0	0	0	0	1
Total	25	19	8	2	1	55
1987, UP2						
Nest found when:						
Building	6	32	10 (8)	1	3	52
Laying	2	3	0	0	0	5
Incubation	9	16	3	0	0	28
Young chicks	2	11	0	0	0	13
OOld chicks	0	0	0	0	0	0
Total	19	62	13	1	3	98

In entries refer to number of nests. The locality UP 2 was not studied in 1985. *In the deserted column the number of nests deserted

Montgomerie 1985). They spend much time sitting, mainly in birch trees, and have a weak *sip* contact call with the parents. They may be led quite far from the natal territory within a few days (we have several records of chicks in association with one or other parent >100 m from territory). Most individuals leave the area within one week of fledging, and only a few independent juveniles and adults were present at these altitudes by mid-July of any year.

TABLE 6
ASSOCIATION OF BROOD SIZE AT HATCHING WITH PROBABILITY OF PREDATION

	Brood size (hatchlings)					
	1985		1986 UP2		1987 UP1	
	<3	>4	<3	>4	<3	>4
Proportion predated	13%	17%	24%	21%	43%	43%
Total number of nests	32	29	25	28	30	14

For each session there was no significant difference in the proportion of nests predated (χ^2 tests), when comparing the two brood size categories.

TABLE 7
ASSOCIATION OF PROBABILITY OF PREDATION WITH LAYING DATE IN THE SEASON

	1985		1986 UP2		1987 UP1	
	Predated	Successful	Predated	Successful	Predated	Successful
Average first egg date	27 May	29 May	11 June	13 June	11 June	11 June
Sample size	8	52	9	39	18	25

When unknown, laying date was back calculated as in Fig. 3. There was no significant difference between the laying date of predated and successful nests in any of the three comparisons (*t*. tests).

FACTORS AFFECTING NESTING SUCCESS

An analysis of whole-brood nesting success is presented in Table 5, separately for each year and area. Predation was often accompanied by the pulling off of the roof or pulling the whole nest out of its socket. Predation was also assumed when the nest was found empty but intact, but in some of these cases the nest may have failed due to starvation of the chicks. Desertions at the egg or nestling stage were assumed when the contents remained. They may have included loss of adults due to mortality. Two other deserted nests containing dead young may have been destroyed by heavy rainfall. Many nests were abandoned during building, and a replacement built nearby: these are listed as desertions in Table 5.

Predation and food availability have been identified as the major factors influencing nesting success and the number of chicks that can be raised to independence (Lack 1968, Lundberg 1985, Lima 1987, Martin 1987). We consider the possible influence of each in turn on the nesting success and timing of breeding of *P. inornatus*.

Predation: Predation rates were sometimes extremely high, and there is little doubt that they were increased by our activity. This was particularly evident at UP1 in 1986 when 64% (N = 28) of all nests found during the building or egg stage were predated, and at UP2 in 1987 when 75% (N = 68) were predated. In both of these study sessions we naively marked the nests we found with red flagging tape, and it appears that the jungle crow *Corvus macrohynchos*, and possibly the Himalayan nutcracker *Nucifraga caryocatactes* learnt to associate the tape with the nest. Because of the unnaturally high predation rates in these two study sessions we do not include them in analyses of factors affecting predation. Corresponding predation rates for the other study sessions were in 1985 at UP1: 16% (N = 31), in 1986 at UP2: 20% (N = 45), and in 1987 at UP1: 40% (N = 40).

Since many nests were found well into incubation, particularly in 1985, predation rates are likely to be generally higher than 20% over the whole breeding cycle (nests were marked with red tape in 1985 and in 1986 at UP2, but apparently avian, predators did not learn to associate the tapes with the nests). We examined variation in the placement of the nest to see if it affected predation probability. Variation in the proportion of nests predated at UP1 in 1987 was examined separately for each of the three classifications of nest location, as recorded in Table 1. In all cases we found no significant associations (χ^2 tests, $P > 0.3$ in each case).

Although crows were probably the major cause of predation, other natural predators are common. We have direct evidence or suspect the following: Himalayan weasel (based on the discovery of the adult parents' wings on or near two predated nests), brown bear *Ursus isabellinus* (based on observing the bear near a nest, and finding an uprooted sapling beside the predated, and removed, nest), and Himalayan nutcracker (observed predating a nest with eggs). In addition the viper *Agkistrodon himalayanus* is common, and was observed preying on a *Phylloscopus occipitalis* nest in the area. Rodents such as mice and voles are possible egg predators, and a redflanked bush robin, *Erithacus cyanurus* was once seen actively chasing a mouse from its nest. Troops of up to 50 Himalayan langurs were seen near recently predated nests.

Predation risks and brood size: It has been suggested that larger broods may be subject to greater predation risk than smaller broods because the parents need to carry food to the young more often, thereby increasing the risk of attracting visual predators (Lack 1968, Lundberg 1985, Lima 1987). We examined this by comparing the proportion of predated nests which had three or fewer hatchlings with the proportion predated which had four or more nestlings, and found no significant difference (Table 6).

Predation risk and laying date: We showed previously that clutches laid earlier in the season take longer to hatch than those laid later. Early nests also appear more exposed, because much of the annual vegetation has still to grow. Early nests may therefore be subject to greater predation risk than those laid later. On the other hand, predation may be less intense earlier in the season, because of the reduced activity of predators, particularly snakes. We found no significant association between laying date and predation risk (Table 7).

Predation was usually manifested as the loss of whole clutches or broods. However, we noticed during routine nest checks that in at least five nests single eggs were being removed or lost through breakage, particularly at UP2 in 1987. In the nest which was most carefully monitored a three egg clutch was reduced to two eggs. The female continued to incubate, and these eggs hatched. We do not know the cause of these egg disappearances.

Replacement nests: Some nests which were predated during early incubation were replaced by second clutches, particularly at UP2 in 1987. On many occasions predation of nestlings is accompanied by complete disappearance of the pair within a few hours, presumably to lower altitudes to begin the moult (Williamson 1974). After some predation events just the female disappears from the area and the male stays on territory continuously singing the *buzz* song. One male was observed carrying food more than 24 hours after its nest had been predated. Most predation events do not appear to lead to the laying of second clutches, and we believe that no second broods are raised after a successful first brood in this population.

Diets and food availability: Late hatching broods often have underweight young (Fig. 5), and starvation was observed in the very last broods to hatch. This may be because late-breeding parents are themselves in poor condition and unable to provide sufficient food, but it may be because food supply is declining towards the end of the season. If this is the case, it could explain why *P. inornatus* breeds early in the season. In this section we assess the possibility by investigating the diet of *P. inornatus* and measures of arthropod availability.

An examination of faecal material and observations of foraging behaviour show that *P. inornatus* is entirely insectivorous. We were unable to quantify arthropod remains in the faeces, but identified Diptera, Coleoptera, Homoptera, Arachnida, and Lepidoptera larvae. Faeces of both adults and nestlings were full with fragments of chitinous appendages, and wings of small arthropods were also common, suggesting that much of the diet consists of adult insects, and the nymphs of hemimetabolous insects. Remains of caterpillars were rare in the faeces. Caterpillars were also rarely observed being eaten: we saw a caterpillar in the bill of the bird in only 2% of all point observations (N = 414).

Feeding techniques did not vary significantly among years or months (Fig. 6). Approximately two thirds of all feeding techniques were standpicks, and most of the remainder were flypicks. Flying insects were rarely captured. Arthropods were picked off branches and leaves, rarely from the trunk, ground, or snow. Most foraging occurs in birch trees, but the understorey willow *Salix denticulata* is commonly utilised, particularly early in the season before the birch is in leaf.

Seasonal changes in plant and arthropod abundance: In 1986 and 1987 leaves began to appear on the birch trees only at the end of May, and by mid-June most trees were in full leaf. In 1985 leaves appeared earlier, but we do not know when.

Changes in the abundance of arthropods captured in the water-detergent plates are shown in Fig.

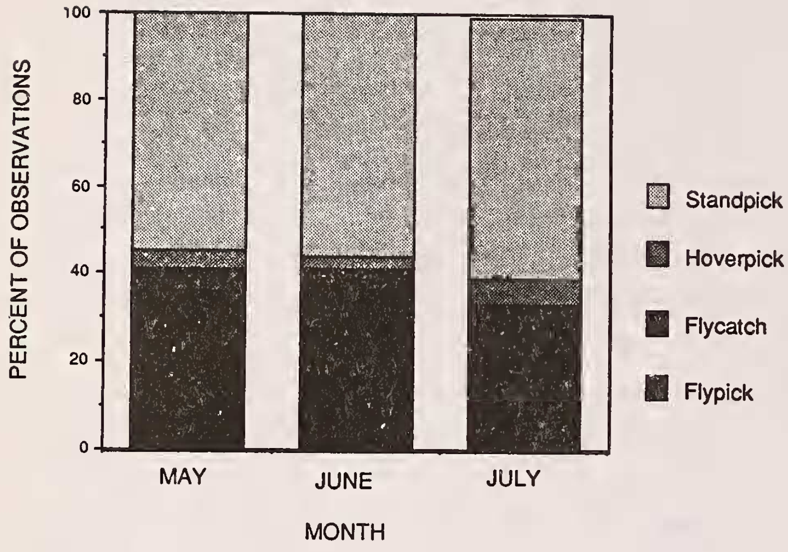


Fig. 6. Proportion of feeding techniques in each of four different categories. There was no significant variation among years (χ^2 tests), and the data were combined for all three years. Sample sizes are May: N = 201 observations, June: N = 135, July: N = 78. There was no significant difference among months in the proportion of foraging techniques used (χ^2 = 2.6, degrees of freedom = 6, P > 0.5)

7. Arthropod abundance appears to be lower in 1986 than the other two years but this is almost certainly an artifact, because the plates were left out for an average of 5.3 days in 1986, but only 1.0 and 1.3 days in 1985 and 1987 respectively. As the plates fill up they are probably less attractive to insects. The plates also occasionally overflowed due to rainfall, or dried out in 1986, but the extent to which this led to lss of insects is unclear (cases of drastic overflows or total drying out are not included in these analyses).

In 1986 there was an increase in arthropod abundance through the season (Fig. 7). There was also a trend towards more arthropods being present in the middle of the season than at the end, although the regression coefficient for the squared term in a second order polynomial regression of arthropod abundance on date was not significant (P = 0.1). In 1987 there was no significant linear increase through the season (Fig. 7) but there was a significant hump in arthropod abundance in the middle of the season (test as before, P<0.05). Thus the results from the plates suggest that flying arthropods tend to be most abundant during the hotter, clear days of June, and less abundant during the more cloudy days of July. The arthropod catch in the plates largely represents Diptera (flies constituted 91% and 96% of the catch in 1986 and 1987 respectively). When Diptera were excluded we found no linear trend in the 1986 season (P> 0.1) but a significant linear increase in catch through the 1987 season [F(1,39) = 5.3, P = 0.03]. When Diptera are excluded there is no hint of a maximum in arthropod abundance in mid-season.

That the possible mid-season maximum in arthropod abundance refers to flying arthropods (i.e., those airborne and able to land in the plates), and not to absolute arthropod abundance is suggested by the collections from the beats of birch

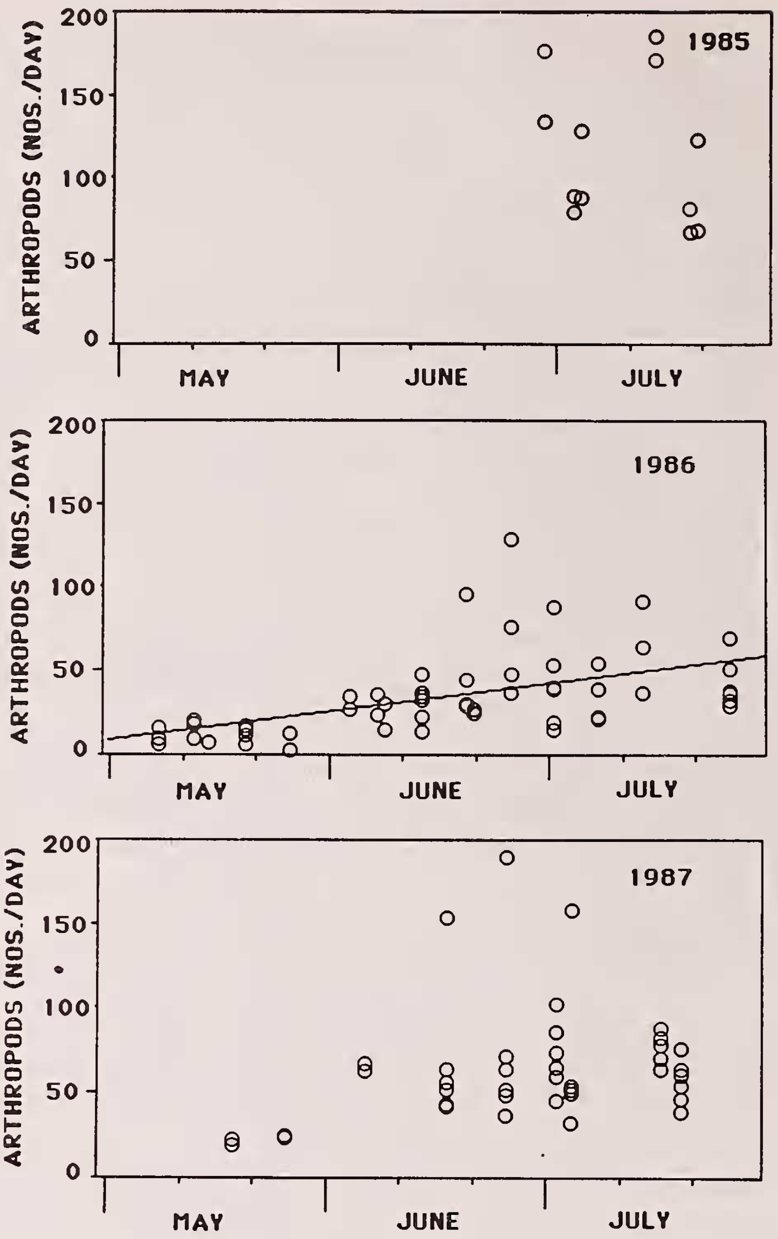
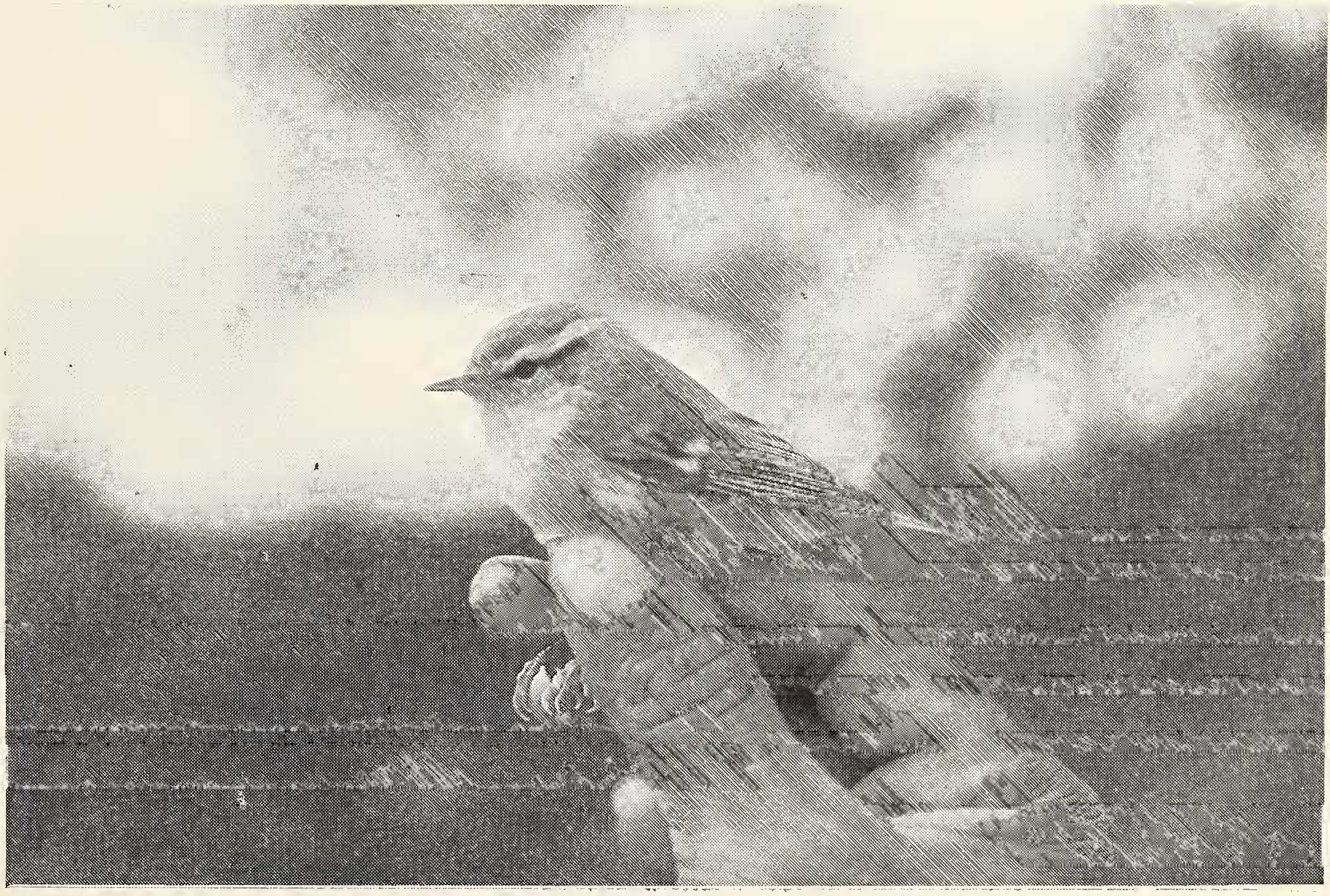


Fig. 7. Seasonal changes in Arthropods found in plates left out for periods of one-six days. Each point marks a single plate, on the day of collection. In 1986 there was a significant increase in abundance through the season, the slope of the linear regression line (shown) is b = 0.55 arthropods/day/day, F (1,56) = 21, P <. 001. In 1987 there was no significant linear increase in abundance, and in 1985 the plates were only put out towards the end of the season. See text for a discussion of curvilinearities in abundance.

Above: Habitat of *Phylloscopus inornatus*
Below: *Phylloscopus inornatus*



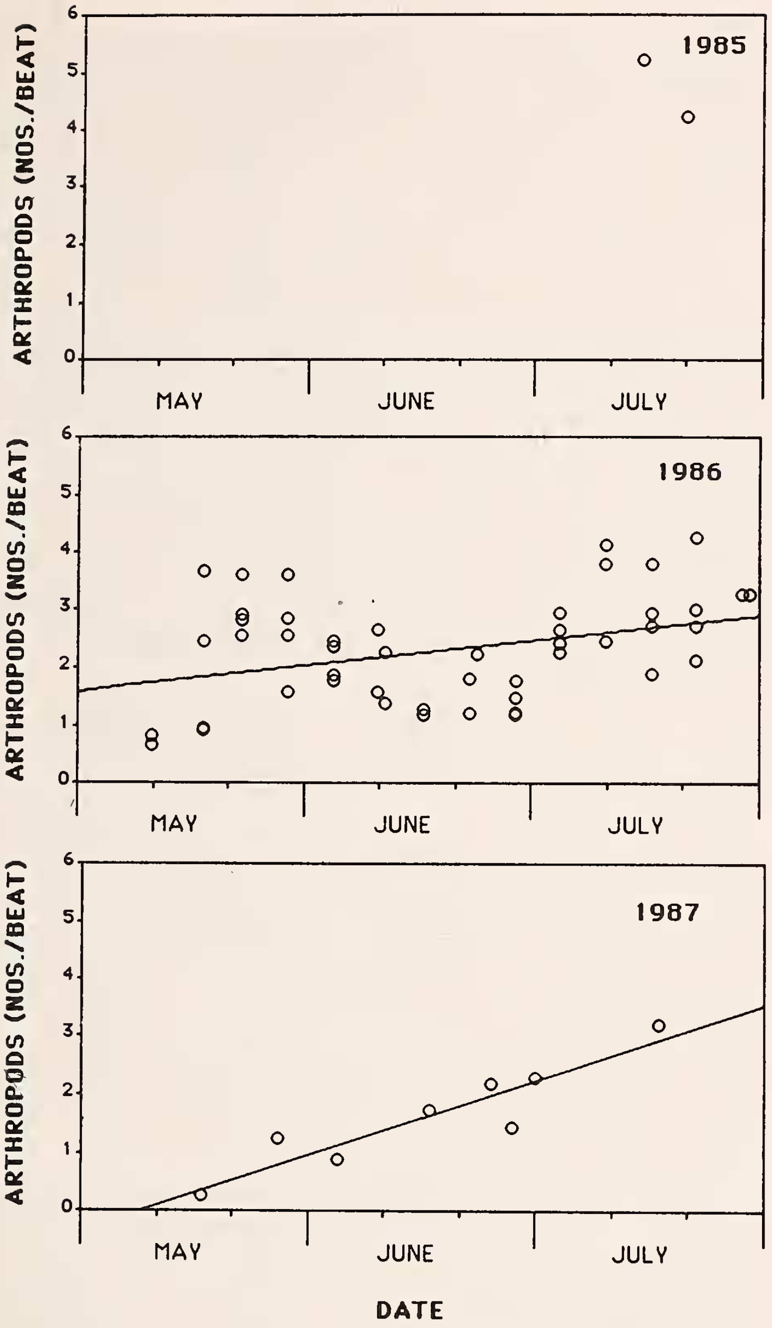


Fig. 8. Numbers of Arthropods falling on to a tray held below a birch branch hit sharply with a stick. Each point refers to the average collection from 20 (occasionally 30) branches in a restricted locality. Linear regression lines for 1986 and 1987 are shown, for which the slopes are
for 1986 b = 0.014 insects/beat/day, F(1,48) = 7, $P < 0.05$,
for 1987 b = 0.025 insects/beat/day, F (1,6) = 34, $P < 0.01$.

branches, which show no evidence of a mid-season maximum (Fig. 8). The proportion of Diptera in the beat collections was 52% in 1986 and 27% in 1987, with much of the remainder being Homoptera. In 1986 the number of arthropods caught by beating increased through the season, but there was an almost significant minimum in June (second order regression, test for the significance of the squared term, P = 0.06). This may reflect the fact that the insects would fly away on sunny days in June, rather than fall on to the tray. In 1987 there was a strong linear increase in arthropod abundance through the season (Fig. 8).

We conclude that arthropod abundance increases from May to July. This does not mean that arthropod availability to birds increases in the same way. As vegetation thickens insects may be more difficult to catch, particularly by flycatching, and there are suggestions that flying insects are in fact less available in July than June.

RETURNS BETWEEN BREEDING SEASONS

Our data on return rates are fragmentary, and cannot be used to infer survival rates. Of 8 females and 10 males breeding in the main study area at UP1 in 1985, one female (13%), and four males (40%) were recorded breeding there in subsequent years (the female and three of these males were recorded in both 1986 and 1987). Of 12 females and 12 males breeding in 1986 four females (33%) and four males (33%) were recorded in 1987. Survival is clearly higher because some birds will be missed, particularly if they disperse between breeding seasons. In many species individuals are more likely to disperse following nest failure (Harvey *et al.* 1979, Newton and Marquiss 1982), and nest failure was common at UP1 in 1986 (Table 5).

Out of 349 banded nestlings in 1985 and 1986 we have found six chicks subsequently breeding in or near the study area. In most bird species young of the year typically disperse further than adults (e.g. Harvey *et al.* 1979, Tiainen 1983).

DISCUSSION

In comparison with species of European *Phylloscopus* warblers *P. inornatus* has a smaller clutch size and breeds at higher density (May 1949, Schonfeld 1978, Lawn 1982, Tiainen 1983). Food availability and/or predation intensity may explain differences in clutch size between Europe and Kashmir. In particular, European species have longer daylight hours in which to forage (Lack 1968). It is not clear that the high density of *P. inornatus* depresses absolute food abundance and affects the clutch size, because some apparent food sources are not exploited. First, several areas of birch trees do not appear to be actively defended or regularly visited (Fig. 1). Second, many conifer trees are not exploited at all, although conifers in territories are regularly visited for feeding.

Clutch size and other measures of reproductive success varied significantly among years. High reproductive success was found in 1985, in which the birds bred early. In a study of a population of *P. trochilus* in Finland Tiainen (1983) showed that the average clutch size decreased during the breeding season in any one year, and that inter-annual differences in clutch size could be largely attributed to differences in clutch initiation date among years. A similar explanation may hold for *P. inornatus*, although we found a significant decline in clutch size with laying date in only one year (1986).

The hypothesis is that females adjust their clutch size according to their condition and their ability to raise young, given the expected food supply at the nestling and fledgling stages (Perrins 1970). A prediction of this hypothesis is that food supply should be absolutely lower at similar stages of the breeding cycle in different years: this remains to be tested.

P. inornatus breeds early and builds its nest as soon as available ground is clear of snow. At times during early incubation there may be severe rain and hailstorms. Three possible adaptations to allow Passerine birds to breed in cold weather have been identified (Carey 1980). First, males may share incubation, although specific examples of this in extreme climates are not known. Second, males may feed the female on the nest, as occurs in crossbills (*Loxia* spp.) (Skutch 1976, Carey 1980). Third, females may leave the nest, and the eggs be able to withstand chilling. This occurs, for example, in North American flycatchers, although the eggs are chilled for a maximum of half an hour once incubation has begun (Morton and Smeraski 1985).

P. inornatus has taken this last adaptation to an extreme not previously recorded in Passerines, with females abandoning the nest, at least during early incubation, for more than 36 hours, during which time the eggs are close to ambient temperature (*c.*9°C). This desertion has no apparent effect on subsequent hatching success. Leaving eggs unattended prior to commencement of incubation is common among birds, but (apart from possible anecdotal examples) periods of extensive abandonment after incubation has begun have only been recorded in a few species of seabirds (Skutch 1976). The Manx shearwater *Puffinus puffinus* has been recorded leaving its eggs unattended for periods of up to seven days with no adverse effects on hatching success (Skutch 1976). In the fork-tailed storm petrel *Oceanodroma furcata* nests may be deserted for several days at a time, and incubation periods vary from 37 to 68 days (Boersma and Wheelwright 1979). These species are larger, and their burrows not as cold.

Typical variation in incubation period appears to be about 2 days for many passerines (Skutch 1976, Ricklefs and Smeraski 1983). Skutch (1976) records a maximum variation of 4 days in the incubation period among 88 Passerine species, with the exception of the red-winged starling *Onychognathus morio*, from the lowlands of South Africa, in which the incubation period varies from 12 to possibly longer than 23 days for unknown reasons (Rowan 1955).

The large variation in incubation period (from 12 to 22 days) in *P. inornatus* probably arises out of variation in the extent to which females can continuously cover the eggs, for incubation period is negatively correlated with laying date, and the earlier the laying the colder the conditions (minimum temperatures average approximately 10°C higher in June than May (Price and Jamdar 1990). Cold temperatures and inclement weather may also account for delays between nest construction and initial laying early in the season.

P. inornatus shows a number of other behaviours which appear to be related to its early breeding. It is possible that the placing of its nest on the ground enables greater insulation than would be the case in trees (Miller 1984), although lack of feathers in the nest reduces insulation properties (Tiainen *et al.* 1983). The species undergoes a diurnal altitudinal migration. Display, nest building, and even the laying of the clutch prior to incubation may occur only in the early hours of the morning, with the majority of the day (and night) spent at lower altitudes.

Our evidence for the diurnal migration is not direct: it is based on the absence of the species in the late morning and afternoons. In the early season there are no leaves on the birch trees and we believe it to be very unlikely that birds were foraging quietly and not noticed. *P. inornatus* individuals were seen at lower altitudes (below 2,800 m) at these times, and we once observed a male flying a long distance down the valley from the UP2 study area, at about 1000 hrs. Although these observations are